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Pelomedusoid Side-Necked Turtles from Late Miocene Sediments in Southwestern Amazonia

EUGENE S. GAFFNEY,¹ KENNETH E. CAMPBELL,² AND ROGER C. WOOD³

ABSTRACT

Fossil turtles have been recovered from outcrops on the Río Purus, Río Acre, and Río Madre de Dios in the southwestern Amazon basin where the borders of Brazil, Peru, and Bolivia converge. The fossils are from two discernible horizons, both probably of late Miocene age and separated by the Ucayali Unconformity. The older horizon is the upper part of the Contamana Group, whereas the younger horizon is Unit A of the Madre de Dios Formation. The Contamana Group has yielded specimens identifiable as *Stupendemys*, a very large podocnemidid reported from Venezuela and

Amazonia, and a new and unnamed taxon of podocnemidid represented only by the lower jaw. It is possible that the lower jaw belongs to *Stupendemys*, but the absence of any associated specimens prevents this assignment. The younger Madre de Dios horizon also yields *Stupendemys*, demonstrating that this large turtle lived both before and after the event that gave rise to the Ucayali Unconformity. A cervical attributable to a large species of *Podocnemis* was found in beds identified as either Unit A or upper Contamana Group.

INTRODUCTION

The pelomedusoid pleurodires or side-necked turtles are an important element in the living fauna of northern South America with two genera and seven species (Iverson, 1992). They also have a long fossil record in this region, extending back to the early Cre-

taceous in Brazil (Gaffney and Meylan, 1991; Meylan, 1996). Numerous records of pelomedusoids throughout the Cretaceous and Tertiary in South America are summarized in de Broin (1988). Ironically, the older pelomedusoid taxa are better known and bet-

¹ Curator, Department of Vertebrate Paleontology, American Museum of Natural History.

² Curator of Ornithology, Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, CA 90007.

³ Professor, Faculty of Sciences and Mathematics, Richard Stockton College of New Jersey, Pomona, NJ 08240.

ter represented in collections than the later forms. Therefore, the relatively fragmentary specimens described here are of importance in helping to reconstruct the history of the Amazonian fauna. In addition to de Broin et al. (1993), Wood (1997) reviewed and described Miocene pelomedusoids from northern South America.

The sparse record of Tertiary pelomedusoids in Amazonia is summarized in de Broin et al. (1993), which also should be seen for a description of pelomedusoid material from the Acre region attributed to *Stupendemys*. More recent studies of large pelomedusoids from this area were made by Bocquentin Villanueva and Negri (1993) and Bocquentin and Silva (1995).

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ABBREVIATIONS

AMNH	American Museum of Natural History, Herpetology
DNPM	Departamento Nacional da Produção Mineral, R�o de Janeiro

LACM	Natural History Museum of Los Angeles County
MCNC	Museo de Ciencias Naturales, Caracas
MCZ	Museum of Comparative Zoology, Harvard
SALMA	South American Land Mammal Age

GEOLOGY

The geology of southwestern Amazonia is characterized by two quite different stratigraphic sequences that are separated by a marked unconformity. The older sequence is known as the Contamana Group (Kummel, 1948) [equivalent to the younger part of the Solimoes Formation in Brazil (Caputo et al., 1971; Maia et al., 1977)], which consists primarily of clays, but also includes some sandstones and channel deposits. These beds are fairly well consolidated and resistant to erosion. They are exposed only during the dry season when the rivers run low, at which time they often form prominent banks or terraces along the rivers. There are no reliable dates on these beds, but faunal evidence indicates an age range of Eocene to late Miocene. The occurrence of fossils in these beds ranges from isolated specimens to large-scale bone beds.

The Ucayali Unconformity separates the Contamana Group from the overlying Madre de Dios Formation (I   Formation in Brazil; Maia et al., 1977), which consists of unconsolidated sands, silts, and clays. This formation is divisible into three informal bodies, Unit A, Unit B, and Unit C, with Unit A being the oldest (Campbell et al., 1985). The basal bed of Unit A is a fossiliferous clay-pebble conglomerate named the Acre Conglomerate Member of the Madre de Dios Formation by Campbell et al. (1985). It is now recognized that this unit is not a legitimate member of the Madre de Dios Formation, but rather a conglomeratic facies within Unit A of the Madre de Dios Formation.

The fossils from the Acre Conglomerate occur as clasts within the conglomerate, and they range in size from millimeters to 1–2 meters in length. Associated skeletal parts are seldom found, and abrasion of some specimens indicates either considerable transport or the effects of having been consumed. Very delicate and yet complete specimens suggest no transport at all. The con-

glomerate was considered for a time to be Upper Pleistocene/Holocene in age based on radiocarbon dates on contained tree trunks (see Campbell and Frailey, 1984; and Campbell and Romero-P., 1989). However, Frailey (1986: 42) assigned a late Miocene (Huayquerian SALMA; 9–6 Ma) age to the fauna from the conglomerate on the basis of known mammalian indicator species. This age assignment was largely made on the basis of the presence of such Huayquerian taxa as *Kiyutherium orientalis* (Francis and Mones, 1965), *Tetrastylus* sp. (Pascual et al., 1966), and possibly *Potamarchus murinus* (Burmeister, 1885). The latter species, however, may have had a Chasicoan (12–9 Ma) to Huayquerian distribution (Pascual et al., 1966). De Broin et al. (1993) suggested that this fauna might be Chasicoan or Huayquerian (late Miocene–early Pliocene in the usage of de Broin et al., 1993). The suggestion of a Chasicoan age by de Broin et al. (1993) was based in part on the presence of *Potamarchus* as cited above. The possibility of an early Pliocene age was based on a tentative biostratigraphic correlation with the “Mesopotamiense” fauna of Argentina. However, a recent paper on this fauna (Noriega, 1995, and papers cited within) places the “Mesopotamiense” in the late Miocene.

The specimens discussed herein are all either from the top of the Contamana Group or the basal conglomerates of the Madre de Dios Formation. The presence of similar taxa in both of these horizons led Frailey (1986) to conclude that the two horizons were close in age and that the fauna of the Acre Conglomerate may have been reworked from the underlying beds. This hypothesis is now considered incorrect, and the fauna of the Acre conglomerate is interpreted to be contemporaneous with the conglomerate, and be late Miocene (Huayquerian SALMA) in age (Campbell et al., in press). The specimens cited by de Broin et al. (1993) as coming from locality LACM 4611 (Acre VI, fig 1) are from the Acre Conglomerate. The geology of southwestern Amazonia has recently been reviewed in detail by Campbell et al. (in press) and readers are referred to that paper for additional information.

SYSTEMATICS

FAMILY PODOCNEMIDIDAE

DISCUSSION: All of the elements described here are identifiable as belonging to the pelomedusoid family Podocnemididae in the sense of de Broin (1988) and Meylan (1996).

Genus indet.

SPECIMEN: Left lower jaw, LACM 141498 (Fig. 2, tables 1 and 2).

LOCALITY: Purus 2. LACM Locality 5994. Known locally as Perserverancia. West bank of Río Purus, State of Amazonas, Brazil. 8°57'32"S; 68°37'10"W.

HORIZON: Contamana Group, probably Ipururo Formation of Kummel (1948).

AGE: Late Miocene Huayquerian SALMA.

COLLECTOR: C. D. Frailey. July 1988.

DESCRIPTION: At a length of 19.6 cm, this lower jaw ramus is the largest pleurodire lower jaw known. Even in a group that has an unusual amount of structural diversity in the feeding mechanisms of its extinct members, this lower jaw stands out. In addition to its large size, the jaw has a unique morphology, being more massive and shorter posteriorly than any other pleurodire lower jaw. Table 1 compares measurements of LACM 141498 with a large jaw of *Peltocephalus*. As there are no standardized (or even previous) measurements of pelomedusoid lower jaws, the measurements and choice of a comparative taxon are fairly arbitrary and intended only as a preliminary basis of comparison.

LACM 141498 is well preserved, with some iron oxide matrix still present in the bottom of the fossa meckelii. The portion of the lower jaw preserved is the nearly complete left ramus. It is possible that the anterior margin of the ramus is broken right at the midline symphysis, but comparison with other jaws suggests that the break, although probably roughly parallel to the midline, may actually be slightly lateral to the actual symphysis. As preserved, the midline projection of LACM 141498 is comparable to that seen in *Podocnemis expansa* and distinctly less than that in *Erymnochelys*. However, as suggested above, the actual symphysis could be missing.

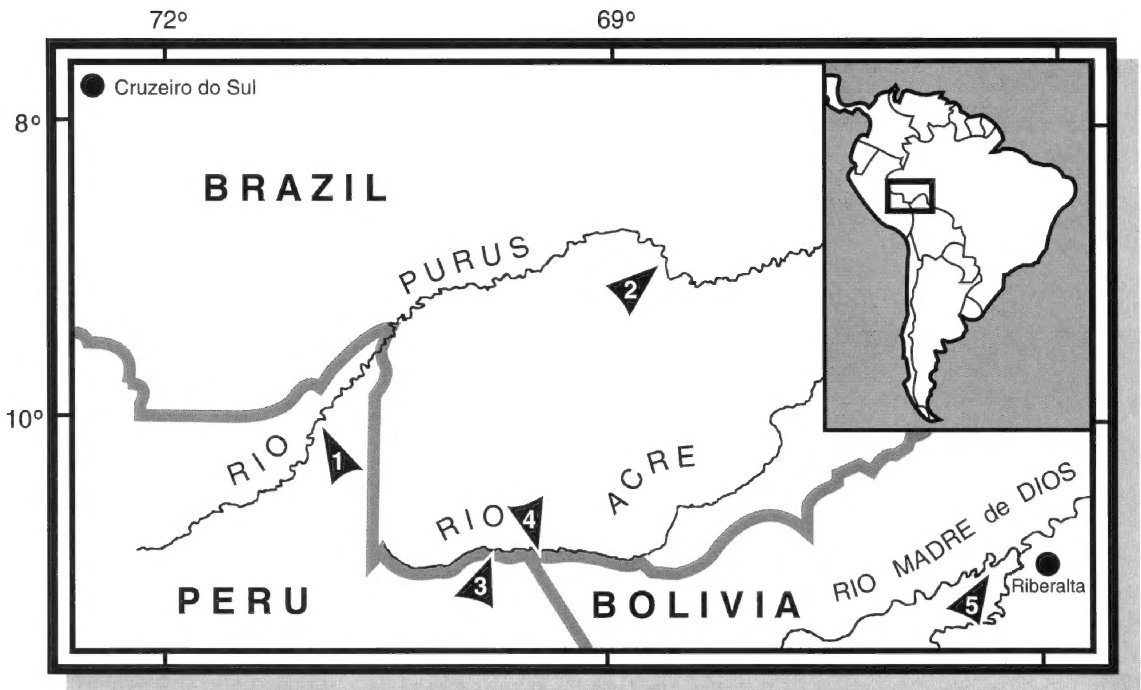


Fig. 1. Map of southwestern Amazonia showing the localities of the fossil turtles described in this paper. 1, LACM locality number 6225, source of LACM 138028 (right scapula). 2, LACM locality number 5994, source of LACM 141498 (lower jaw). 3, LACM locality number 4418, source of LACM 131946 (nuchal) and LACM 131947 (first thoracic vertebra). LACM locality number 4611 (Frailey, 1986: fig. 3) lies just west of 4418 and was the source of pelomedusoid fossils described by de Broin et al. (1993). 4, LACM locality number 5158, source of LACM 131949 (fourth cervical vertebra). 5, LACM locality number 6072, source of LACM 137948 (cervical vertebra).

The lower jaw of pleurodires, fossil and recent, is poorly known. The only pleurodire lower jaw described in detail is *Podocnemis expansa* by Fuchs (1931). Fortunately, LACM 141498 is most similar to this genus, at least among the jaws available to us at present. Other good figures of *Podocnemis expansa* are in Gray (1855; reprinted in Gaffney, 1979) and Hay (1908). Because the lower jaws of fossil pleurodires are not well described, we will focus our comparisons of LACM 141498 on the recent pelomedusoids, particularly *Podocnemis expansa*. (Table 2 summarizes some characters in LACM 141498 and the recent pelomedusoids.)

The triturating surface consists mostly of a relatively deep, oval concavity, deeper than in *Podocnemis* or any known living or extinct pleurodire. The labial ridge is curved and more acute than in *Podocnemis*. The lingual ridge is a blunt margin, sloping dorsally to the prominent accessory ridge. The acces-

sory ridges of LACM 141498 and *Podocnemis expansa* both lie on a shelf, but otherwise they are quite different. In LACM 141498 the ridge is acute, but it is blunt in *Podocnemis*. The ridge tapers in width and disappears anteriorly in *Podocnemis*, while in LACM 141498 it increases in height and width anteriorly and ends abruptly short of the midline in a distinct dorsal projection.

The coronoid process of LACM 141498 is relatively high and acute in comparison to that of *Podocnemis*. The coronoid bone margins are not clear in LACM 141498, but one suture on the medial surface appears to be between dentary and coronoid and indicates that, as in *Podocnemis*, the coronoid of LACM 141498 forms part of the lingual ridge anterior to the coronoid process. The fossa meckelii in all living pleurodires has a dorsal opening that is slitlike and relatively narrow. The dorsal opening in LACM 141498, however, is huge. The fossa meck-

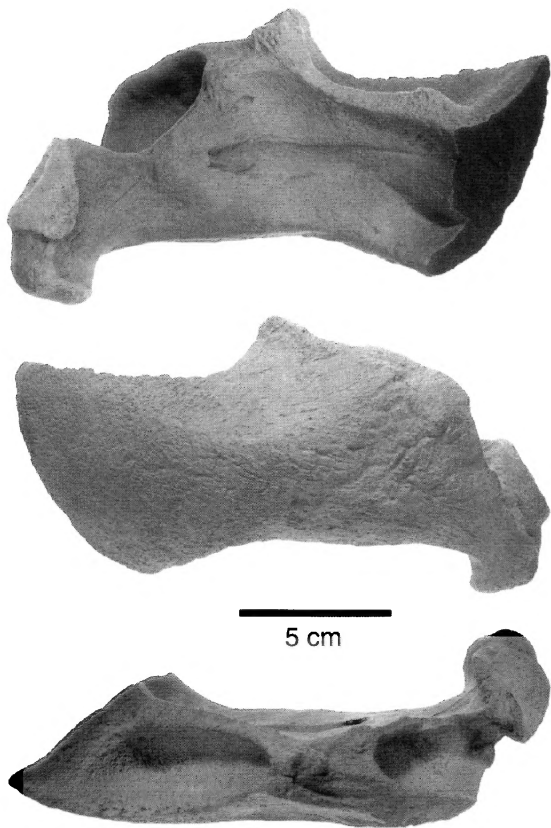


Fig. 2. Left lower jaw of unnamed podocnemid turtle, LACM 141498, Rfo Purus, Brazil. **Top**, medial view. **Middle**, lateral view. **Bottom**, dorsal view.

elii itself is usually much larger than its dorsal opening in most turtles. In LACM 141498, however, the dorsal opening is the size of the fossa, which is also unusually large. The fossa meckelii in LACM 141498 fills the posterior end of the jaw to such an extent that the area articularis mandibularis forms part of the posterior margin, and the fossa opens posterolaterally next to the jaw articulation. This implies a very large main adductor tendon and associated musculature.

LACM 141498 can be identified as a pleurodire because it has a roughly hemispherical area articularis mandibularis in contrast to the median longitudinal ridge usually found in cryptodires (Gaffney, 1979: 217). There is considerable variation in this feature in turtles, however, and a better indication of relationships lies in other features of the jaw. The recent species of the genus *Podocnemis* have a well-developed ventral tubercle at the posterior end of the jaw, below the area articularis mandibularis. This is probably best identified as a processus retroarticularis despite its ventral position (also termed the processus subarticularis by Fuchs, 1931), because it does bear the attachment for the m. depressor mandibulae. This structure and the adjacent area articularis mandibularis are very similar in both the living *Podocnemis* and LACM 141498. Both taxa are also distinguished from other living pleurodires by an accessory ridge paralleling the lingual ridge. On the basis of these features we can identify this jaw as belonging to the family Podocnemididae with a fair degree of cer-

TABLE 1
Comparison of Lower Jaw (in cm)

Measurement	LACM 141498	MCZ 93077 <i>Peltocephalus dumeriliana</i>
Total length along long axis of jaw	19.6	7.8
Height of jaw at processus coronoideus	8.2	2.5
Width of triturating surface just anterior to processus coronoideus	2.6	1.0
Width of triturating surface at symphysis	5.6	1.3
Width of symphysis measured at right angles to long axis of jaw	4.7	2.3
Maximum length of fossa meckelii	6.0	1.5
Maximum width of fossa meckelii	2.8	0.2
Width of jaw at processus coronoideus	3.9	1.2
Width of area articularis mandibularis	3.8	1.4
Length from processus coronoideus to posterior end of jaw measured along long axis of jaw	9.8	3.6

TABLE 2
Comparison of LACM 141498 with the Lower Jaw in Recent Pelomedusoids

Character	LACM 141498	<i>Podocnemis</i>	<i>Peltocephalus</i>	<i>Erymnochelys</i>	<i>Pelusios</i>	<i>Pelomedusa</i>
Jaw strongly telescoped, short, deep, and heavy	yes	no	no	no	no	no
Fossa meckelii unusually large and open dorsally	yes	no	no	no	no	no
Processus retroarticularis well developed	yes	yes	yes	yes	no	no
Processus retroarticularis directed ventrally	yes	yes	no	no	no	no
Accessory ridge	present	present	absent	absent	absent	absent
Accessory ridge with tooth-like projection	yes	no	no	no	no	no
Symphysis	indet	fused	fused	fused	fused	sutured
Foramen dentofaciale majus lies anterior to processus coronoideus	no	yes	yes	yes	yes	yes

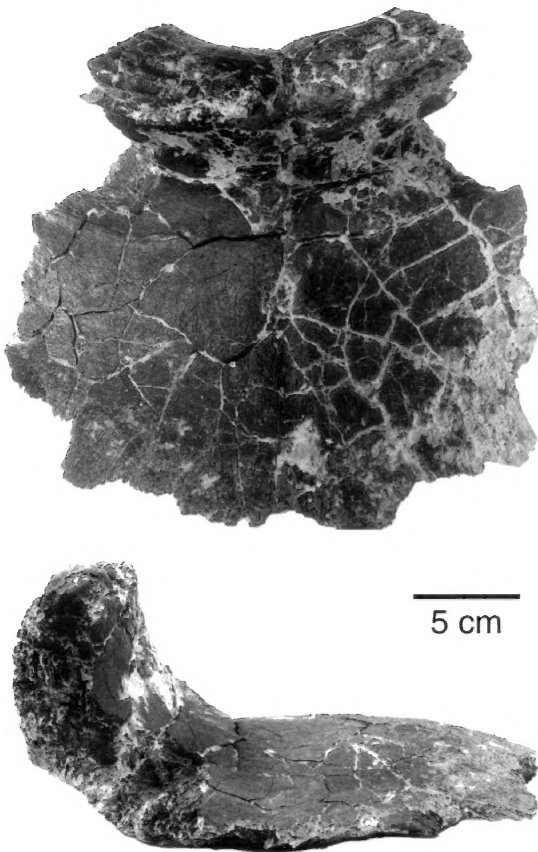


Fig. 3. Nuchal of *Stupendemys* sp., LACM 131946, Río Acre, Peru. **Top**, dorsal view (anterior toward top of page). **Bottom**, left lateral view (anterior toward left).

tainty. Confirmation could only come from associated skull or postcranial elements.

Aside from being a *Podocnemididae* related particularly to *Podocnemis*, this lower jaw gives no further information on its possible identity. It would appear that this specimen is not the lower jaw of the large skull from the Río Jurua, Acre, Brazil, in the DNPM, MCT 1496R, because they both seem to have unique but noncomplementary triturating surface configurations. This skull, considered by de Broin et al. (1993) as a possible candidate for the still unknown skull of *Stupendemys*, is a *podocnemidid* with large, tusk-like projections on the labial ridges and a thick, massive skull. MCT 1496R could be the skull of *Stupendemys*. Conversely, the lower jaw described here could also be from *Stupendemys*. As the jaw and skull do not seem to belong to the same taxon, we either have *Stupendemys* plus one new taxon represented by the skull or the jaw, or we have *Stupendemys* plus two new taxa.

Stupendemys sp.

SPECIMEN: Nuchal Bone, LACM 131946 (fig. 3).

LOCALITY: Acre I. LACM Locality 4418. West bank of Río Acre, Provincia de Tahuamanu, Departamento de Madre de Dios, Peru. 10°56'S; 60°50'W.



Fig. 4. Right scapulae of *Stupendemys* in anterior views with the acromial process of the scapula horizontal and the dorsal process of the scapula vertical. **Left**, MCZ 4376 (also in Wood, 1976: fig. 5), Urumaco, Venezuela. **Right**, LACM 138028, Río Purus, Peru.

HORIZON: Contamana Group, probably Ipururo Formation of Kummel (1948).

AGE: Late Miocene. Huayquerian SALMA.

COLLECTOR: K. E. Campbell and C. D. Frailey; August, 1977.

DESCRIPTION: The most distinctive element in *Stupendemys* is the nuchal bone. The two specimens described by Wood (1976) have nuchals with a dorsally curved margin that forms a large flange or collar at right angles to the main plate of the nuchal. In the type, MCNC 244, the curvature stops short of being recurved and the margin is thin. In MCZ 4376 the curvature turns and folds back to a certain extent. The edge is also thicker than in MCNC 244.

In the Acre specimen, LACM 131946, the curvature is developed to about the same extent seen in MCNC 244 and it does not recurve. However, LACM 131946 has a thick margin, similar to MCZ 4376. In both LACM 131946 and MCZ 4376 the thickened areas are bisected by the sulcus between the first marginals so that there are two projec-

tions on the anterodorsal margin of the nuchal.

Stupendemys sp.

SPECIMEN: Scapula, LACM 138028 (fig. 4).

LOCALITY: Purus 94–9. LACM Locality 6225. Río Alto Purus, Provincia de Purus, Departamento de Ucayali, Peru. 10°17'16"S; 71°04'10"W.

HORIZON: Basal conglomerate (Acre conglomerate) of Unit A of the Madre de Dios Formation.

AGE: Late Miocene. Huayquerian SALMA.

COLLECTOR: K. E. Campbell, C. D. Frailey, and L. Romero-Pittman. July 22, 1994.

DESCRIPTION: The specimen is a portion of a right scapula consisting of the glenoid and adjacent parts of the dorsal scapular process and the acromial process. The distal ends of the scapular processes are broken off. Although cracked in places, the preservation of the bone is quite good; there is no evidence

of crushing or distortion. Wood (1976) described the scapular material found with the type specimen of *Stupendemys*, MCZ 4376. Both right and left scapulae and coracoids are preserved, facilitating comparisons with the Peruvian specimen.

The scapula of *Stupendemys* is unique among pelomedusoids in having a dorsal scapular process that is strongly bowed with a flattened flange projecting laterally from the main axis. The illustration of the *Stupendemys* shoulder elements in Wood (1976: fig. 5) is mistakenly labeled as scapula plus coracoid when it is actually the scapula alone. The complete right and left shoulder girdles in MCZ 4376 show that Wood's figure 5 is the anterior view of the left scapula in that specimen rather than the ventral view of a scapula plus coracoid. *Pelusios* and *Podocnemis* in Wood's figure 5 are ventral views of coracoids plus scapulae and are correct as labeled (see also Gaffney, 1990: fig. 138D, for a ventral view of scapula plus coracoid in *Podocnemis*). Thus, Wood's figure 5 (1976) shows the dorsal scapular process and its expanded lateral flange. The glenoid of *Stupendemys* faces roughly anteroventrolaterally, as in *Podocnemis*.

LACM 138028 agrees closely with the right scapula in MCZ 4376 and is readily identified as a right scapula. LACM 138028 has a dorsal scapular process that is strongly bowed and has a flattened lateral flange, both features that are known only in *Stupendemys*. Only the proximal part of the flange is preserved in LACM 138028, but it is very distinctive. The coracoid articulation is in the same position in both LACM 138028 and MCZ 4376. The bone is crushed and distorted more in MCZ 4376 than in LACM 138028, but there does seem to be a difference independent of preservation. The angle between the dorsal scapular process and the acromial process is slightly greater in LACM 138028 than in MCZ 4376. It is unlikely that this alone indicates a separate taxon.

Measurements of the dorsal scapular process base (5.6 cm in LACM 138028, 7.3 cm in MCZ 4376) and acromial process base (5.2 cm in LACM 138028, 7.0 in MCZ 4376) indicate that LACM 138028 was from an individual about $\frac{3}{4}$ the size of MCZ 4376.

cf. *Stupendemys*

SPECIMEN: Cervical vertebra, LACM 137948.

LOCALITY: Madre de Dios I. LACM Locality 6072. Known locally as Candelaria, south bank of Río Madre de Dios, Provincia de Madre de Dios, Departamento de Pando, Bolivia. 11°02'47"S; 66°16'35"W.

HORIZON: Basal conglomerate (Acre conglomerate) of Unit A of the Madre de Dios Formation.

AGE: Late Miocene Huayquerian SALMA.

COLLECTOR: K. E. Campbell. August 18, 1985.

DESCRIPTION: LACM 137948 is a very worn cervical vertebra preserving only the centrum; the neural spine and all zygapophyses are broken off. Although the specimen is too poorly preserved to determine its numerical position in the cervical series, which is difficult enough in pelomedusoids, it is likely to be a more posterior cervical because it is relatively massive. LACM 137948 has a midline centrum length of 11.2 cm, which is longer than that of the Venezuelan *Stupendemys* specimens and apparently longer than the cervicals figured in de Broin et al. (1993: pl. 2). It is not possible to predict how vertebral proportions would change if some species of *Podocnemis* were scaled up to the size of *Stupendemys*. It is possible that some of these large, massive cervicals belong to *Podocnemis* rather than *Stupendemys*. However, it is more likely that the morphological differences between *Podocnemis* and *Stupendemys* are not entirely size dependent. In that case, these more massive cervicals, which lack the central restrictions proximal to the articulations seen in living species of *Podocnemis*, can be assigned to *Stupendemys*.

The cervicals described by Wood (1976) and clearly associated with *Stupendemys* specimens differ from those of other pelomedusoids. As noted by de Broin et al. (1993), the well-developed saddle-shaped central articulations show that *Stupendemys* was a podocnemidid. In most podocnemidids, the central articular surfaces, particularly the posterior ones, extend out beyond the main body of the centrum. The centrum itself is relatively narrow and excavated lat-

erally (Williams, 1950: fig. 11; Gaffney, 1990: fig. 109). In *Stupendemys* the centra are more massive, and the central articular facets are close to the main body of the centrum.

cf. *Podocnemis* sp.

SPECIMEN: Fourth cervical vertebra, LACM 131949.

LOCALITY: Cachuela Bandeira. LACM Locality 5158. South bank of Río Acre, Provincia Nicolas Suarez, Departamento de Pando. 10°3'48"S; 69°31'24"W.

HORIZON: Either a channel deposit in top of Contamana Group (Ipuru Formation) or basal Acre conglomerate of Unit A of Madre de Dios Formation. The outcrop at this locality consists only of consolidated, ferruginously cemented sandstones in the bottom and sides of the river channel, so it is impossible to place the fossiliferous sandstone into a stratigraphic context with certainty. We consider it most probable that the sandstone is within the Contamana Group.

AGE: Late Miocene Huayquerian SALMA, regardless of which of the two possible horizons listed above is correct.

COLLECTOR: K. E. Campbell. June 20, 1981.

DESCRIPTION: Except in size, this cervical is nearly identical to the fourth cervical of *Podocnemis expansa*. The centrum between the main body and the posterior articulation surface is a bit thicker than in *Podocnemis*, but it is still distinctly different from the short, massive centra of *Stupendemys*. The fourth cervical in *Podocnemis expansa* (AMNH 62947) is 2.8 cm long, whereas LACM 131949 is 5.7 cm long. This is further evidence that very large specimens of *Podocnemis* were present in the late Tertiary of the Amazon Basin (Williams, 1956; de Broin et al., 1993).

Gen. et sp. indet.

SPECIMEN: First thoracic vertebra, LACM 131947.

LOCALITY: Acre I. LACM 4418. As above.

HORIZON: Contamana Group, probably Ipururo Formation of Kummel (1948).

AGE: Late Miocene Huayquerian SALMA.

COLLECTOR: K. E. Campbell and C. D. Frailey. August, 1977.

DESCRIPTION: This specimen consists of the anterior half of a first thoracic vertebra that bears the prezygapophyses and central articulation. The vertebra is very similar to the same bone in *Podocnemis*. It bears a concave, roughly triangular central articulation, with no signs of a saddle shape. The prezygapophyses face anteromedially, very much as in *Podocnemis expansa*. The first thoracic of *Stupendemys* is not known. LACM 131947 is 5.1 cm across at the maximum width of the central articulation, compared with a width of 1.6 cm for the same measurement in a specimen of *Podocnemis expansa*, AMNH 62947. The plastron of AMNH 62947 is 57 cm long (the carapace is damaged), whereas Wood (1976, table 3) estimated one of the *Stupendemys* plastra (MCNC 245) as 76 cm in length. It is possible that this vertebra is from a shell as large as or larger than that of *Stupendemys*. Although it is not possible to identify this vertebra to genus, it is another record of large pelomedusoids at this site.

SUMMARY

The upper reaches of the Amazon, along the Río Purus, Río Acre, and Río Madre de Dios, have yielded fossils of side-necked turtles. These fossils are from two stratigraphic horizons, an upper (Madre de Dios Formation, Unit A) and a lower (Contamana Group, upper part) separated by the Ucayali Unconformity. Both horizons are probably late Miocene in age. Postcranial material consisting of vertebra, scapula, and nuchal, are identified as *Stupendemys*, a very large podocnemidid known only from the postcrania.

A large and massive lower jaw has characters allying it with the podocnemidids and *Podocnemis* in particular, despite its unique morphology. The shortened posterior part, deep triturating trough, gigantic fossa meckelii, and cusped accessory ridge make it unique among pleurodires. Although this specimen is possibly the lower jaw of *Stupendemys*, it appears to be distinct from an undescribed and unassociated skull from the same age and area (which could itself be the

skull of *Stupendemys*). Thus, in addition to *Stupendemys*, there is evidence for at least one (and possibly two) large, undescribed

podocnemidid species in this area in the late Miocene, as well as a large species of the recent genus, *Podocnemis*.

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